

Polygyrid Land Snails, *Vespericola* (Gastropoda:
Pulmonata), 1. Species and Populations Formerly
Referred to *Vespericola columbianus*
(Lea) in California

by

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Abstract. *Vespericola columbianus pilosus* (Henderson, 1928) and *V. columbianus orius* (Berry, 1933) differ from typical Pacific Northwest *V. columbianus* (Lea, 1838) in shell and reproductive system characters and are separated as distinct species. A new species, *Vespericola marinensis*, is described and compared to *V. pilosus* and *V. columbianus*. Other California records based on shells of the *V. columbianus* type are summarized.

INTRODUCTION

This is the first in a projected series of studies on the systematics of the West American polygyrid land snail genus *Vespericola* Pilsbry, 1939. The greatest species diversity occurs in northwestern California and southwestern Oregon, where nine species have been named. One additional species is described herein. In addition, two species formerly regarded as subspecies of *Vespericola columbianus* (Lea, 1838) are shown to differ in genital characters from typical *V. columbianus* and are separated as distinct species. The material treated in this and following papers was collected by the authors from 1968 to 1991; additional material of many of the new taxa was located in museum collections. As remarked earlier (ROTH, 1985), the reproductive system in species of *Vespericola* is often more strongly differentiated than the shell. In many cases, shell characters are adequate for identification. However, especially in the complex of species resembling *Vespericola megasoma* (Pilsbry, 1928), dissection of the mature reproductive system is sometimes necessary for a firm identification. With specimens from new localities, it is always desirable to establish the species' identity by dissection.

Vespericola columbianus pilosus (Henderson, 1928), the type species of *Vespericola*, differs anatomically (and somewhat in shell characters) from *V. columbianus* from the valley of the Columbia River, Washington-Oregon, and

accordingly is separated as a distinct species. Its distribution, limited to central California, is reviewed. Populations in Marin County, differing in shell and anatomical characters from those on the San Francisco Peninsula, are described as a new species, *V. marinensis*. *Vespericola columbianus orius* (Berry, 1933) differs anatomically and conchologically from *V. columbianus* and is considered a separate species. Remaining Californian records based on shells of the *V. columbianus* type (*i.e.*, those in which the inner part of the basal lip curves or angles forward in basal view and the inner lip is not markedly dilated over the umbilicus) are summarized as a basis for future investigation.

MATERIALS AND METHODS

Shell height and diameter are vernier caliper measurements and exclude the expanded lip of mature shells. Whorls were counted by the method of PILSBRY (1939:xi, fig. B). The density of periostracal setae was estimated by counting the number of setae per square millimeter on the shoulder of the body whorl, 0.25 whorl behind the aperture of adult specimens, at 30× magnification under a dissecting microscope with an ocular reticle. Three counts were taken per specimen and the mean (to the nearest integer) recorded.

Specimens for dissection were prepared by the method of MILLER (1967). Snails were first drowned in water to

insure expansion and relaxation, then heated to a temperature of 60°C, at which time the bodies could be pulled easily from the shells and dissected. After the body cavity was opened, the position and maturity of the reproductive system were observed; then the whole reproductive system was removed, attached to a small patch of body wall around the external genital orifice. The penis was slit longitudinally to expose the verge and the pilasters and papillae on the wall of the penial chamber. The verge of at least one specimen of every species was completely excised for examination.

Whole mounts of genitalia were prepared by the method of MILLER (1967): stained with hematoxylin, dehydrated and cleared in successive baths of ethanol and toluene, and mounted on slides with Permount mounting medium. Organ measurements were taken from mounted specimens. Anatomical drawings were made by projecting the image of the whole mount on paper with an overhead projector.

Shell growth in Polygyridae is determinate and ends with, first, a constriction of the body whorl and then a turning outward and thickening of the lip. Reproductive maturity normally seems to follow a short time after the lip turns, but the presence of a turned lip does not guarantee a reproductively mature specimen. Therefore, at least a portion of each sample was kept alive in a terrarium for a period of weeks or months before dissection to ensure full development of the genital structures. Terraria consisted of redwood boxes with screened tops. A 3–6 cm layer of soil and leafmold from the collecting locality was added. Specimens were fed lettuce. There is no indication that growth of *Vespericola* in terraria under these conditions is in any way abnormal.

The following abbreviations are used: ANSP, Academy of Natural Sciences of Philadelphia; BR, senior author's collection, San Francisco, California; CAS, California Academy of Sciences; LACM, Los Angeles County Museum of Natural History; SBMNH, Santa Barbara Museum of Natural History; UCM, University of Colorado Museum; USNM, United States National Museum of Natural History, Smithsonian Institution.

SYSTEMATICS

Family POLYGYRIDAE Pilsbry, 1895

Vespericola Pilsbry, 1939

Vespericola PILSBRY, 1939:xvii; PILSBRY, 1940:892–894; ZILCH, 1960:586.

Type species: *Polygyra columbiana pilosa* Henderson, 1928 [= *Vespericola pilosus* (Henderson)], by original designation.

Polygyridae with shell small to medium-sized, globose to depressed-helicoid, narrowly umbilicate to imperforate. Periostracum smooth, matte-surfaced, or granulose, bearing sparse to densely set setae (or at least their scars). Base of last 0.2 turn of body whorl more or less compressed upward; strong constriction present behind lip. Parietal

lamella present or absent (sometimes variably present within a species). Lip turned outward and sometimes reflected. No lamellae present on outer or basal lips, but low basal callus sometimes present. Epiphallus internally ridged, markedly narrower than apex of penis, usually with swollen, sausage-shaped upper section, terminating in bound, vestigial epiphallic caecum at junction of epiphallus and vas deferens. No penial gland present. Penial retractor muscle inserted on epiphallus, distant from penis. Retentor muscle originating on epiphallus or branching from penial retractor near epiphallus, inserting on summit of well developed penial sheath. Upper part of penial chamber bearing V-shaped pilasters or diverging rows of papillae; or, entire wall of chamber covered with close-set papillae. Paired longitudinal pilasters absent. Smooth, conical, spoon-shaped, or needle-like verge extending forward from summit of the penial chamber, containing seminal duct, with terminal or subterminal pore, without terminal papillae. Much of penis inserted into everted spermathecal duct in copulation; basal penis slightly expanded into small clasping disk. Verge directed forward during copulation.

Spider webs, soil, and bits of plant debris often adhere among the setae, forming a dark crust; the resulting appearance of the shell is cryptic and may mimic a mammal dropping.

The principal species-level diagnostic features of the reproductive system are the length of the atrium; the shape and dimensions of the penial complex, including the verge; the shape and size of the spermatheca (“gametolytic gland,” “bursa copulatrix”) and its duct; and the presence or absence of a fleshy thickening at or near the base of the spermathecal duct.

EMBERTON (1988, *e.g.*) does not recognize an epiphallus (as distinct from the proximal part of the vas deferens) in Triodopsinae. We follow the convention of PILSBRY (1940) and other authors in terming as epiphallus the portion of the seminal duct from the insertion of the epiphallic caecum (“flagellum”) to the apex of the penis.

The noun *Vespericola* is of masculine gender, so adjectival species names often end in *-us*.

The genus ranges around the northeast Pacific rim from the Aleutian Islands to San Luis Obispo County, California.

The family-group name Polygyridae Pilsbry, 1895, is junior to Mesodontidae Tryon, 1866. A petition to validate the better-known name Polygyridae (EMBERTON, 1989) has been affirmed (ICZN, 1992).

Vespericola pilosus (Henderson, 1928)

(Figures 1–6)

Polygyra columbiana pilosa HENDERSON, 1928:143; PILSBRY, 1928:181–182, 185 (in part), figs. 10, 10a; HENDERSON, 1929:80 (in part; *non* Alaska and Pacific Northwest records, and probably *non* fig. 35); HENDERSON, 1936:255 (reference to California localities only).

Vespericola columbiana pilosa (Henderson): PILSBRY, 1939:



Explanation of Figures 1 to 3

Figures 1-3. *Vespericola pilosus* (Henderson). Shell, BR 1648, CALIFORNIA: San Mateo County: N slope of San Bruno Mountain facing Guadalupe Canyon, B. Roth coll., 4 June 1989. Top, apertural, and basal views. Diameter 13.9 mm.

xvii; PILSBRY, 1940:896-898 (in part), figs. 513:10, 513:10a (non figs. 512C, 512D); INGRAM, 1946:92 (in part); INGRAM & LOTZ, 1950:25-26 (in part), pl. 5, figs. 5, 6; LA ROCQUE, 1953:309 (in part).

Vespericola pilosa (Henderson): BAKER, 1962:16.

Non *Vespericola columbiana pilosa* (Henderson): WEBB, 1970:75-77.

Non *Vespericola columbiana* var. *pilosa* (Henderson): EYERDAM, 1951:7.

Diagnosis: A medium-sized *Vespericola* with depressed-helicoid to conical, narrowly umbilicate shell, 5.5-6.3 whorls, 19-30 periostracal setae/mm², and usually no parietal lamella. Penis elongate-conical, ratio of protruding part to sheathed part approximately 0.87; verge 0.5-0.6 mm long, conical, ending in 0.1 mm opposing lips.

Description of shell: Shell medium-sized for the genus (diameter 12.3-15.5 mm) depressed-helicoid to conical, narrowly umbilicate, with 5.5-6.3 whorls. Spire straight-sided or weakly convex; whorls rounded, suture moderately impressed. Embryonic whorls 1.5-1.7, with prominent, rather coarse, radial wrinkling; wrinkles surmounted by smooth, hemispheric to radially elongate papillae. Early teleoconch whorls with inconspicuous, crowded, retractive growth rugae and irregular granulation with collabral trend. Periostracum bearing slender setae in gently descending rows; setae 19-30/mm², approximately 0.2-0.25 mm long on spire and shoulder of body whorl, erect or curving away from direction of coiling, broadened at base. Surface between setae sharply microscopically granulose on spire (smoother on body whorl) and finely radially wrinkled. Periphery broadly rounded. Base tumid, papillose where setae worn off; setae shorter than on spire, extending into umbilicus. Umbilicus contained about 14 times in diameter. Body whorl weakly to moderately deflected downward, constricted behind lip. Aperture broadly auriculate; peristome shallowly concave in profile, at angle of about 35° to shell axis. Lip turned outward and reflected, especially at base; basal lip sometimes with faint, elongate internal thickening. Parietal lamella usually absent (but present in the holotype and in San Francisco Presidio population). Inner part of basal lip straight or gently curved

forward, moderately dilated, covering about half of umbilicus. Periostracum warm brown; lip pinkish buff.

Description of soft anatomy: Eight specimens from San Bruno Mountain (regarded as virtual topotypes for the reasons discussed below) were dissected.

Color of living animals tan to brown, darker and grayer on body-stalk. Mantle over lung 10-50% maculated with black.

Atrium (Figure 4) of moderate length for genus. Penis elongate-conical, with anterior, basal portion enclosed in thin sheath adnate to base. Penial retractor muscle inserted on epiphallus. Retentor muscle extending from penial retractor muscle at attachment on epiphallus to summit of penial sheath, from which other thin retentor fibers form connections with parts of epiphallus and vas deferens. Interior of penial chamber bearing papillose pilasters in diverging V-pattern (Figure 5). Slender peduncular section of about 2.0 mm present between base of sheath and junction with atrium.

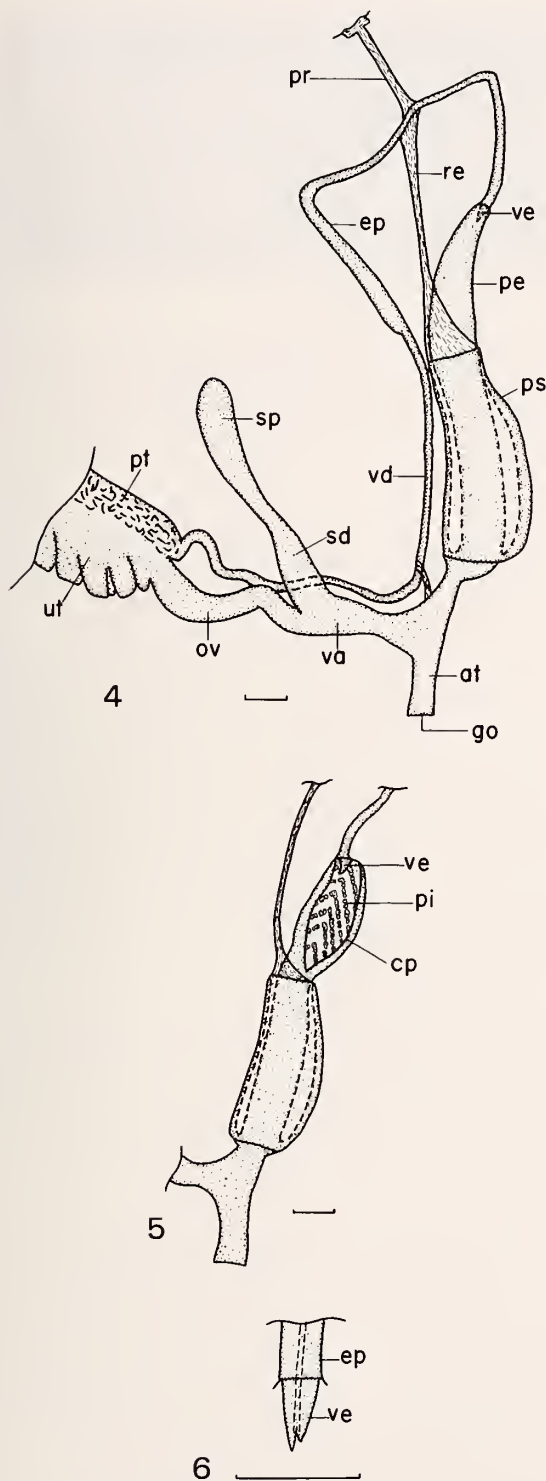
Sheathed part of penis in specimen shown in Figure 4 about 5.0 mm in length, protruding part about 3.5 mm. In other specimens from same locality, sheathed part varying from 4.0 to 5.4 mm (mean 4.5 mm); protruding part varying from 3.4 to 4.6 mm (mean 3.9 mm). Mean ratio of protruding length to sheathed length about 0.87.

Apex of penis containing short, conical, pointed verge 0.5 mm long and 0.3 mm wide at base. Seminal duct opening into penial chamber at tip of verge; tip of verge split into two opposing lips about 0.1 mm long (Figure 6).

Spermathecal duct relatively small and narrow, tightly appressed to free oviduct (which is smaller in diameter and branches from it), cylindrical-conic, about 2.5 mm long, about 1.0 mm in diameter at junction with oviduct, tapering gradually to 0.4 mm constriction at base of spermatheca.

Spermatheca elongate-ovate, rather slender in fully mature specimens, narrowly cylindrical in less mature individuals, about 3.5 mm long, with rounded tip.

Type material: Holotype: ANSP 11142a (BAKER, 1962). Paratype: UCM 16202 (WU & BRANDAUER, 1982).



Explanation of Figures 4 to 6

Figures 4-6. *Vespericola pilosus* (Henderson). Drawings made from projections of stained whole mounts. Figure 4. Anterior portion of reproductive system, SBMNH 36089, CALIFORNIA: San Mateo County: N slope of San Bruno Mountain facing Guadalupe Canyon, W. B. Miller coll., 24 August 1991. Figure 5. Penis with protruding portion opened to show verge and pa-

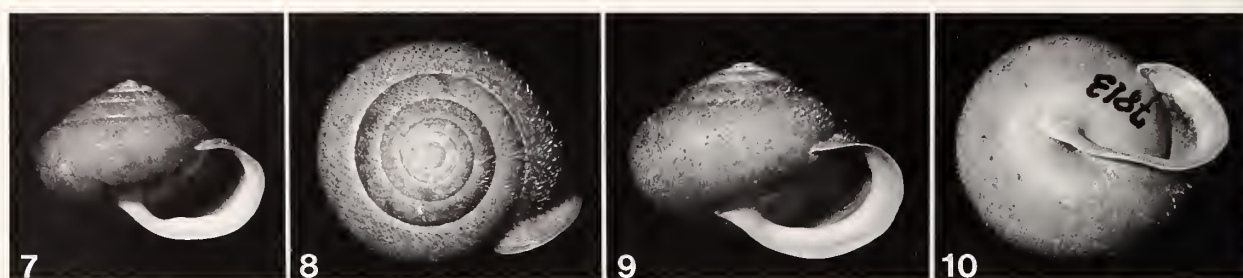
Distribution: CALIFORNIA: San Francisco City and County (ANSP, SBMNH, UCM): Presidio (CAS); Lobos Creek (CAS); near Mountain Lake (CAS); Golden Gate Park (CAS); Lake Merced (CAS). San Mateo County: N slope of San Bruno Mountain facing Guadalupe Canyon (BR, SBMNH); Colma (BR, CAS); Half Moon Bay (SBMNH); canyon back of Half Moon Bay (CAS); Pilarcitos Creek (CAS); Purisima Creek Canyon near mouth of Walker Gulch (BR); San Gregorio (CAS).

Remarks: The type locality of *Vespericola pilosus* is San Francisco, with no more exact location specified. The species is not known to have been collected within the city limits of San Francisco in recent years; we have searched the San Francisco localities cited above, and others, without finding it. Given the extent of habitat modification in the urban environment, it is unlikely that the type population is still extant. However, the species is moderately common on San Bruno Mountain in northern San Mateo County, just across the county line from San Francisco. The coastal brushfield and chaparral vegetation there was at one time continuous with that of the San Miguel Hills of south-central San Francisco. We have therefore based our shell and anatomical observations on samples from San Bruno Mountain and consider them to represent typical *V. pilosus*.

Previous authors used the name *Vespericola* (or *Polygyra*) *columbiana pilosa* to refer to samples with setose periostracum, whatever their provenance. The name was not applied in the sense of a geographically delimited subspecies. HENDERSON (1928:143) stated, "this race ranges from Alaska to San Francisco Co., Cal." A periostracum with setae occurs in specimens from Alaska to central California and is, in fact, the predominant condition throughout the range of *V. columbianus*. Topotypic and near-topotypic specimens of *V. columbianus* collected by the junior author are setose. We have not yet located any populations characterized by absence of setae, and consider the taxonomic significance of this character to be undemonstrated.

However, specimens from San Francisco and vicinity differ in reproductive system anatomy and details of shell shape from samples from farther north. Populations from the San Francisco peninsula (which include the type population of *Polygyra columbiana pilosa* Henderson) are here assigned to *Vespericola pilosus*, which is separated as a distinct species; populations from Marin County are described as a new species, *V. marinensis*. We provisionally

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pillose pilasters, SBMNH 36090, collection data same as above. Figure 6. Verge and part of epiphallus, showing seminal duct in dashed lines with opening between apical lips, SBMNH 36091, collection data same as above. Abbreviations for anatomical figures: at, atrium; cp, cut edge of penis; ep, epiphallus; go, genital orifice; ov, oviduct; pe, penis; pi, pilaster; pr, penial retractor; ps, penial sheath; pt, prostate; re, retentor; sc, cavity of penial sheath; sd, spermathecal duct; sp, spermatheca; ut, uterus; va, vagina; vd, vas deferens; ve, verge. Scale lines in anatomical figures = 1 mm.



Explanation of Figures 7 to 10

Figures 7–10. *Vespericola columbianus* (Lea). Figure 7. Shell, SBMNH 36092, WASHINGTON: Clark County: Ridgefield Wildlife Refuge, near Vancouver, under log along trail, W. B. Miller coll., 21 July 1989. Diameter 12.1 mm. Figures 8–10. Shell, SBMNH 36093, WASHINGTON: Pacific County: right bank of Columbia River 0.4 km W of highway bridge to Astoria, Oregon, W. B. Miller coll., 12 July 1989. Top, apertural, and basal views. Diameter 14.0 mm.

refer records from northwestern California and the Pacific Northwest to *V. columbianus*, *sensu lato*, pending a more comprehensive study of the anatomy of samples from throughout its range.

An attempt was made to collect topotypes of *Vespericola columbianus* at Vancouver, Washington. Although the area has been extensively urbanized, one specimen was collected at the Ridgefield Wildlife Refuge north of the city (Figure 7). Upon dissection, its anatomy was found to be too immature for comparative measurements. The following anatomical notes are based on mature specimens collected about 130 km downstream along the right (north) bank of the Columbia River just west of the highway bridge to Astoria, Oregon (Figures 8–10).

Color of living animals tan, darker and grayer on body-stalk. Mantle over lung clear buff, about 20% maculated with black.

Atrium (Figure 11) of moderate length for genus. Penis elongate-conical, largely enclosed in thin sheath adnate to base. Penial retractor muscle inserted on epiphallus. Narrow retentor muscle extending from penial retractor muscle at attachment on epiphallus to summit of penial sheath, from which other thin retentor fibers form connections with parts of epiphallus and vas deferens. Interior of penial chamber bearing papillose pilasters in diverging V-pattern (Figure 12). Broad peduncular section of about 1.0 mm present between base of sheath and junction with atrium.

Sheathed part of penis about 5.0 mm in length; protruding part about 0.2 mm. Apex of the penis containing short, conical, pointed verge 1.0 mm long and 0.5 mm wide at base. Seminal duct opening into penial chamber at tip of verge through minute slit (Figure 13).

Spermathecal duct short and massive, appressed to free oviduct (which is smaller in diameter and branches from it), cylindrical-conic, about 2.0 mm long, about 1.5 mm in diameter at junction with oviduct, tapering sharply to 0.5 mm constriction at base of spermatheca.

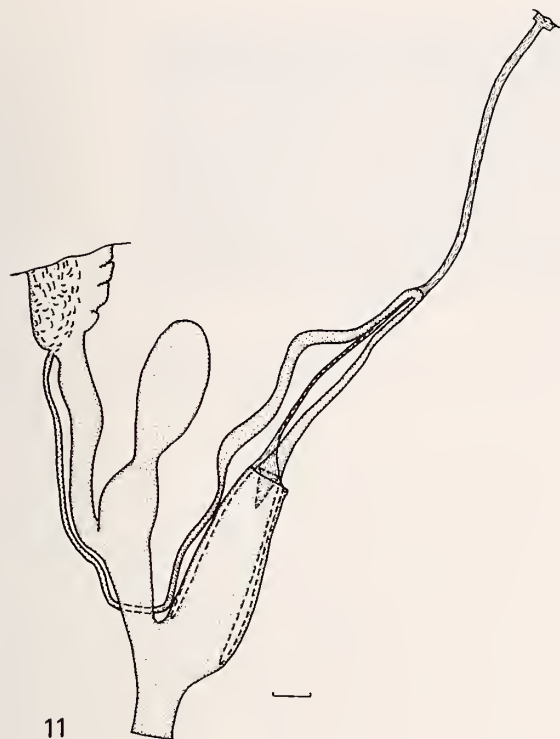
Spermatheca oblong-ovate in fully mature specimens, narrowly cylindrical in less mature individuals, about 4.0 mm long, with rounded tip.

Numerous additional specimens of *Vespericola columbianus* were examined, ranging from Prince Rupert and the Queen Charlotte Islands, British Columbia, to the valley of the Columbia River, Washington-Oregon. A consideration of the variation within the species over its range is beyond the scope of this paper. However, a summary of characters based on 69 dissected specimens is as follows: mantle over the lung 10–90% maculated with black; sheathed part of penis 3.6–8.5 mm long (mean 5.7 mm); protruding part of penis 0–1.4 mm long (mean 0.6 mm). (In seven specimens from three localities in British Columbia [Bridal Veil Falls, Hope District; Port Hardy, Vancouver Island; and Graham Island, Queen Charlotte Islands], penial sheath extending 0.5–4.2 mm above summit of penis.) Verge 0.8–2.0 mm long; spermathecal duct 1.5–3.0 mm long.

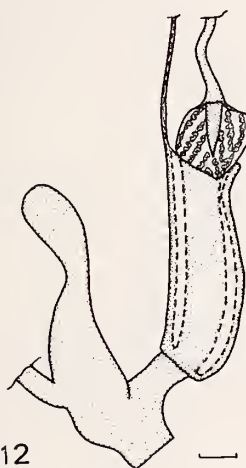
The main anatomical characters that distinguish *Vespericola columbianus* are its stout penial complex, with the sheath completely or almost completely enveloping the penis in mature specimens, and the moderately long, conical, pointed verge at the apex of the penial chamber. The spermathecal duct is short and thick at its junction with the oviduct.

Vespericola pilosus differs anatomically from *V. columbianus* by the long protruding portion of its penis, its much shorter verge, and its narrower, more slender spermathecal duct and spermatheca. It is distinguished from *V. marinensis*, next described, by having the sheathed length of the penis equal to or greater than the protruding length, a verge half or less the length of the verge of *V. marinensis*, and a more slender spermathecal duct. Table 1 summarizes the major differences among these taxa.

The periphery of the shell of *Vespericola pilosus* is broadly rounded; that of *V. columbianus* is usually weakly subangulate to at least the last 0.5 whorl. The periostracal setae of *V. pilosus* tend to be denser (19–30/mm²) than those of *V. columbianus* (7–19/mm² in the specimens examined) and much denser than in *V. marinensis* (7–10/mm²). PILSBRY (1940) considered the typical form of *V. columbianus* generally to lack setae, but all specimens we have



11



12



13

seen have (or originally had) setae, although they have been rubbed off some museum specimens.

The habitat of *Vespericola pilosus* includes moist spots in coastal brushfield and chaparral vegetation; under leaves of cow-parsnip (*Heracleum lanatum*); around spring seeps; in leafmold along streams; and in alder woods.

The earlier citation of the taxon as "*Vespericola pilosa*" by BAKER (1962) was not a taxonomic revision but merely a convention of that publication, a list of type material in the ANSP.

For purposes of the American Fisheries Society list of the common names of mollusks (TURGEON *et al.*, 1988) and other administrative uses, we propose the name "brushfield hesperian."

Vespericola marinensis Roth & Miller, sp. nov.

(Figures 14–19)

Vespericola columbiana pilosa (HENDERSON): PILSBRY, 1940: 896–898 (in part; records from Marin County, California, only); INGRAM, 1946:92 (in part); INGRAM & LOTZ, 1950:25–26 (in part). *Non Vespericola pilosus* (HENDERSON, 1928).

Diagnosis: A small to medium-sized *Vespericola* with depressed-helicoid to broadly conical, narrowly umbilicate shell, 5.4–5.9 whorls, 7–10 periostracal setae/mm², and no parietal lamella. Penis elongate-conical, ratio of protruding part to sheathed part approximately 1.6; verge 0.7–1.8 mm long, conical, ending in 0.1 mm opposing lips.

Description of shell: Shell small to medium-sized for the genus (diameter 10.5–15.0 mm) depressed-helicoid to broadly conical, narrowly umbilicate, with 5.4–5.9 whorls. Spire straight-sided or very weakly convex; whorls rounded, suture moderately to strongly impressed. Embryonic whorls 1.5–1.8, with prominent, sharp to rounded, radial wrinkles surmounted by smooth, hemispheric to radially elongate papillae. Early teleoconch whorls with inconspicuous, crowded, retractive growth rugae and close-set, regular granulation with collabral trend. Periostracum bearing slender setae in diagonal, often steeply descending, rows; setae 7–10/mm², approximately 0.3–0.35 mm long

Explanation of Figures 11 to 13

Figures 11–13. *Vespericola columbianus* (Lea). Drawings made from projections of stained whole mounts. Figure 11. Anterior portion of reproductive system, SBMNH 36094, WASHINGTON: Pacific County: right bank of Columbia River just W of highway bridge to Astoria, Oregon, W. B. Miller coll., 12 July 1989. Figure 12. Penis with protruding portion opened to show verge and papillose pilasters, SBMNH 36095, BRITISH COLUMBIA: Naikoon Provincial Park, Graham Island, Queen Charlotte Islands, W. B. Miller and E. S. Miller coll., 22–24 June 1991. Specimen slightly immature as indicated by small spermatheca and penial sheath not enveloping entire penis. Figure 13. Verge and part of epiphallus, showing seminal duct in dashed lines with opening in apical slit, SBMNH 36096, collection data same as for preceding specimen.



Explanation of Figures 14 to 16

Figures 14–16. *Vespericola marinensis* Roth & Miller, sp. nov. Shell, holotype, SBMNH 36080, CALIFORNIA: Marin County: Bear Valley Trail, Point Reyes, W. B. Miller coll., 23 April 1990. Top, apertural, and basal views. Diameter 12.2 mm.

on spire and shoulder of body whorl, erect or curving away from direction of coiling, sometimes with recurved tip, moderately broadened at base. Surface between setae densely, smoothly granulate on spire and body whorl and collabrally wrinkled. Periphery simply rounded, not subangulate. Base tumid, densely papillose; with setae extending into umbilicus. Umbilicus contained about 13–16 times in diameter. Body whorl deflected downward except immediately behind aperture, sharply constricted behind lip. Aperture broadly auriculate; peristome shallowly concave in profile, at angle of 25° to 45° to shell axis. Lip turned outward and expanded, somewhat reflected at base; basal and outer lips sometimes thickened submarginally. Parietal lamella absent. Inner part of basal lip gently angled forward, weakly to moderately dilated, covering $\frac{1}{3}$ to $\frac{1}{2}$ of umbilicus. Periostracum warm brown; lip pale tan to white.

Dimensions of holotype: Diameter (exclusive of expanded lip) 12.2 mm, height 8.7 mm, whorls 5.6.

Description of soft anatomy: The holotype and 66 additional specimens were dissected.

Color of living animals tan to brown on foot, darker and grayer on body-stalk. Mantle over lung 15–30% maculated with black.

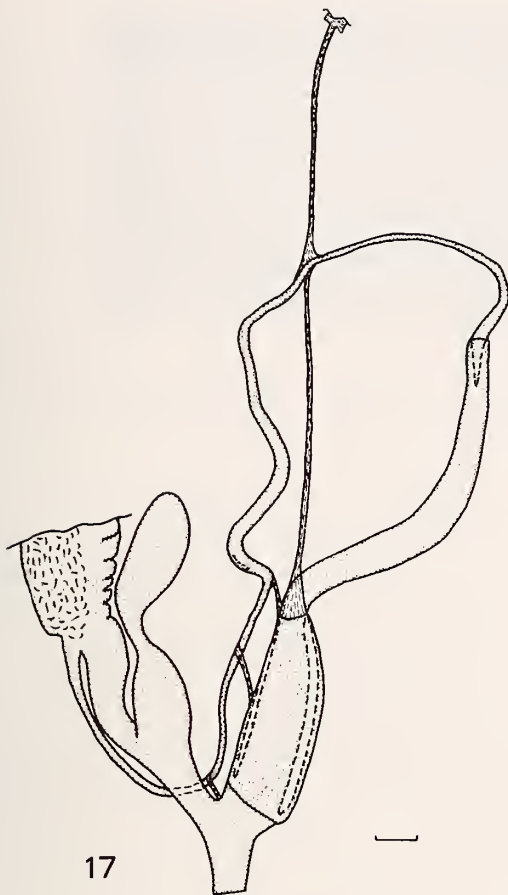
Atrium (Figure 17) of moderate length for genus. Penis elongate-conical, anterior, basal portion enclosed in thin sheath adnate to base. Penial retractor muscle inserted on epiphallus. Narrow retentor muscle extending from penial retractor muscle at attachment on epiphallus to summit of penial sheath, from which other thin retentor fibers form connections with parts of epiphallus and vas deferens. Interior of the penial chamber bearing papillose pilasters in diverging V-pattern (Figure 18). Short, broad peduncular section of about 0.8 mm present between base of sheath and junction with atrium.

Sheathed part of penis in specimen shown in Figure 17 about 4.8 mm in length, protruding part about 8.8 mm. In remaining specimens, sheathed part varying from 3.4

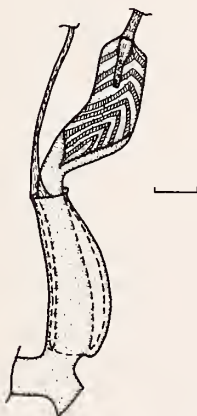
Table 1

Summary of dimensions (in mm), ratios, and selected characters in *Vespericola columbianus*, *V. pilosus*, *V. marinensis*, and *V. orius*. Statistics are range with mean in parentheses. Only adult specimens included.

Character	<i>V. columbianus</i>	<i>V. pilosus</i>	<i>V. marinensis</i>	<i>V. orius</i>
Mantle over lung, coverage by dark maculation	10–90%	10–50%	15–30%	30–40%
Sheathed part of penis	3.6–8.5 (5.7)	4.0–5.4 (4.5)	3.4–6.0 (4.4)	2.5–3.0 (2.7)
Protruding part of penis	0.0–1.4 (0.6)	3.4–4.6 (3.9)	4.8–10.8 (7.0)	—
Ratio of protruding part to sheathed part	mean \approx 0.11	mean \approx 0.87	mean \approx 1.6	—
Verge, length	0.8–2.0 (1.2)	0.5–0.6 (0.5)	0.7–1.8 (1.1)	0.15–0.20 (0.18)
Verge, end	minute slit	apical slit forming 0.1 mm lips	apical slit forming 0.1 mm lips	conical
Spermathecal duct	1.5–3.0 (2.6), massive	2.5, slender	\approx 3.0, massive	\approx 2.0, slender
Spermatheca, length	4.0	3.5	3.2	\approx 2.7
Peduncular section of penis	1.0	2.0	0.8	1.0
Periphery	weakly subangulate	broadly rounded	broadly rounded	usually weakly subangulate
Periostracal setae/mm ²	7–19	19–30	7–10	11–17



17



18



19

to 6.0 mm (mean 4.4 mm); protruding part varying from 4.8 to 10.8 mm (mean 7.0 mm). Mean ratio of protruding length to sheathed length about 1.6.

Apex of penis containing short, conical, pointed verge varying from 0.7 to 1.8 mm long, 0.3 mm wide at base. Seminal duct opening into penial chamber at tip of verge through apical slit which forms two opposing lips about 0.1 mm long (Figure 19).

Spermathecal duct massive, tightly appressed to free oviduct (which is smaller in diameter and branches from it), cylindrical-conic, about 3.0 mm long, about 1.3 mm in diameter at junction with oviduct, tapering gradually to 0.4 mm constriction at base of spermatheca.

Spermatheca oblong-ovate in fully mature specimens, narrowly cylindrical in less mature individuals, about 3.2 mm long, with rounded tip.

Type material: Holotype: SBMNH 36080 (shell and dissected anatomy), CALIFORNIA: Marin County: Bear Valley Trail, Point Reyes, W. B. Miller coll., 23 April 1990.

Paratypes: SBMNH 36081 (4 shells and stained whole mount of reproductive system), from same locality as holotype. Additional paratypes (all, CALIFORNIA: Marin County:), SBMNH 36082 (4), along Bear Valley Trail ca. 2.0 km inland from Arch Rock, under logs and bark, W. B. Miller coll., 1 January 1989. SBMNH 36083 (1), along Bear Valley Trail, ca. 0.8 km from Arch Rock, W. B. Miller coll., 25 July 1989. SBMNH 36084 (1), along Bear Valley Trail, ca. 0.8 km from Arch Rock, under log, W. B. Miller coll., 20 September 1990. SBMNH 36085 (2), Bear Valley Trail, W. B. Miller and E. S. Miller coll., 24–29 April 1988. SBMNH 36086 (7), Bear Valley Trail, between Wilderness boundary and Arch Rock, under logs along trail, W. B. Miller coll., 13 November 1989. Paratypes also deposited in ANSP, CAS, LACM, and USNM.

Referred material: CALIFORNIA: Marin County: Dillon Beach (CAS); Tomales Point (CAS); head of first large east-draining draw N of Whites Gulch (BR, SBMNH), McClures Beach parking area (BR), side canyon of Home Ranch Creek Canyon (BR), Muddy Hollow Trail (SBMNH); Kehoe Beach (BR, SBMNH) (all, Point Reyes Peninsula); Inverness (BR, SBMNH); Point Reyes Station (CAS); Olema Creek (BR); 1.6 km SW of California Hwy. 1 bridge over Walker Creek, E side of Tomales Bay

Explanation of Figures 17 to 19

Figures 17–19. *Vespericola marinensis* Roth & Miller, sp. nov. Drawings made from projections of stained whole mounts. Figure 17. Anterior portion of reproductive system of holotype, SBMNH 36080, CALIFORNIA: Marin County: Bear Valley Trail, Point Reyes, W. B. Miller coll., 23 April 1990. Figure 18. Penis with protruding portion opened to show verge and papillose pilasters, SBMNH 36087, CALIFORNIA: Marin County: Muddy Hollow Trail, Point Reyes, W. B. Miller coll., 20 April 1990. Figure 19. Verge, SBMNH 36088, CALIFORNIA: Marin County, Alpine Dam, W. B. Miller and B. Roth coll., 16 January 1991.



Explanation of Figures 20 to 22

Figures 20–22. *Vespericola orius* (Berry). Shell, BR 330, CALIFORNIA: El Dorado County: Eagle King Mine, Grizzly Flats, E. P. Chace and E. M. Chace coll., autumn 1938. Top, apertural, and basal views. Diameter 13.0 mm.

(BR); Walker Creek, 0.4 km above mouth of Chileno Creek (BR); Taylorville (SBMNH); San Geronimo Creek near Forest Knolls (BR); Mesa Road, ca. 3 km NW of Bolinas (BR, SBMNH); debris above high tide line, N end of Bolinas Lagoon (BR) Lagunitas Creek, 0.3 km below Alpine Dam (BR, SBMNH); Alpine Dam (SBMNH); near Stinson Beach (CAS); near Fairfax (CAS); Ross (SBMNH); San Rafael (CAS); Muir Woods (CAS); Sausalito (SBMNH); Point Bonita (CAS).

Remarks: In the type material, adult shell diameter ranges from 11.6 to 14.0 mm (mean of 24 specimens including holotype, 12.57 mm); height, 8.0 to 9.5 mm (\bar{x} = 8.65 mm); height-diameter ratio, 0.63 to 0.73 (\bar{x} = 0.689); number of whorls, 5.4 to 5.9 (\bar{x} = 5.68). The largest shells examined are from Walker Creek, 0.4 km above mouth of Chileno Creek, reaching 15.0 mm in diameter and 9.6 mm in height. Small shells, adult at 10.5 mm diameter, occur on the northern part of the Point Reyes Peninsula, as at Tomales Point and near Whites Gulch.

The shell of *Vespericola marinensis* differs from that of *V. pilosus* and *V. orius* in having fewer setae per millimeter and in having the surface between the setae densely covered by smooth, round to radially elongated granules. In *V. pilosus* the granulation is sharper on the spire, usually becoming weak or obsolete on the body whorl. In *V. orius* granulation is weak throughout.

Vespericola marinensis is distinguished anatomically from other species by its moderately long, pointed verge, with apical slit forming two opposing lips, in a narrowly elongated penis protruding for more than half of its length from the basal penial sheath. It differs from *V. pilosus* by its longer verge (more than twice the length of the *V. pilosus* verge) and by its longer protruding part of the penis. It differs from *V. columbianus* by the much longer protruding part of the penis, which is never completely enclosed by the penial sheath.

The habitat includes moist spots in coastal brushfield and chaparral vegetation; under leaves of cow-parsnip (*Heracleum lanatum*); around spring seeps; in leafmold along streams; in alder woods; and in mixed evergreen forest.

INGRAM & LOTZ (1950) reported *Vespericola columbiana pilosa* from Hacienda, Sonoma County. PILSBRY (1928) reported it (as *Polygyra*) from Russian River, presumably in Sonoma, rather than Mendocino, County. We have not examined specimens from these localities, and do not know whether they represent northern records of *V. marinensis*. The occurrences are within the range of *Vespericola megasoma* (Pilsbry, 1928).

For purposes of the American Fisheries Society list of the common names of mollusks (TURGEON *et al.*, 1988) and other administrative uses, we propose the name “*Marin hesperian*.”

Etymology: The species is named for Marin County.

Vespericola orius (Berry, 1933)

(Figures 20–24)

Polygyra columbiana oria BERRY, 1933:15, pl. 2, figs. 11, 11a.
Vespericola columbiana oria (Berry): PILSBRY, 1940:900–901,
fig. 516; INGRAM, 1946:92.

Diagnosis: A medium-sized *Vespericola* with depressed-helicoid to broadly conical, umbilicate shell, 5.2–6.25 whorls, 11–17 periostracal setae/mm², and no parietal lamella. Penis short, stout, completely enclosed in sheath, apical portion slender and tubular, containing 0.15–0.20 mm long, conical verge.

Description of shell: Shell thin, medium-sized for the genus (diameter 11.6–16.4 mm) depressed-helicoid to broadly conical, umbilicate, with 5.2–6.25 whorls. Spire straight-sided or very weakly convex; whorls rounded, suture moderately impressed. Embryonic whorls 1.5–1.8, most often with prominent, sharp, radial wrinkles surmounted by smooth, round to radially elongate papillae, but wrinkles sometimes faint and surface between papillae smooth. Early teleoconch whorls with inconspicuous, crowded, retractive growth rugae, very slightly granular. Periostracum bearing slender setae in gently descending rows; setae 11–17/mm², approximately 0.3 mm long on spire and shoulder of body whorl, erect or curving away

from direction of coiling, not greatly broadened at base but sometimes with triangular basal lamina abaperturally. Surface between setae finely radially wrinkled, locally with patches of minute granulation. Periphery usually with a trace of angulation, at least before last 0.5 whorl; sometimes simply rounded. Base tumid, with setae shorter than on spire, extending into umbilicus. Umbilicus contained 11–14 times in diameter. Body whorl weakly to moderately deflected downward, constricted behind lip. Aperture broadly auriculate; peristome shallowly concave in profile, at angle of about 35° to shell axis. Lip turned outward and reflected, especially at base; not conspicuously thickened. Parietal lamella absent. Inner part of basal lip curved or angled forward, moderately dilated, covering $\frac{1}{5}$ to $\frac{1}{2}$ (usually $\frac{1}{3}$ or less) of umbilicus. Periostracum warm brown; lip pinkish buff.

Description of soft anatomy: Twelve specimens were dissected.

Color of living animals tan, darker and grayer on body-stalk. Mantle over lung clear buff, 30–40% maculated with black.

Atrium (Figure 23) of moderate length for genus. Penis short and stout, completely enclosed in thin sheath adnate to base. Apical part of penis slender and tubular, of same diameter as epiphallus, containing minuscule verge. Sheath extending above summit of penis, enclosing portion of epiphallus. Penial retractor muscle inserted on epiphallus. Narrow retentor muscle extending from penial retractor muscle at attachment on epiphallus to summit of penial sheath, from which other thin retentor fibers form connections with parts of epiphallus and vas deferens. Short peduncular section of about 1.0 mm present between base of sheath and junction with atrium.

Length of penis, from base to verge, in figured specimen about 2.5 mm; sheathed part of epiphallus about 1.3 mm; total sheath length 3.8 mm. In other specimens, length of penis varying from 2.5 to 3.0 mm (mean 2.7 mm; total length of the sheath varying from 3.4 to 4.2 mm (mean 3.9 mm).

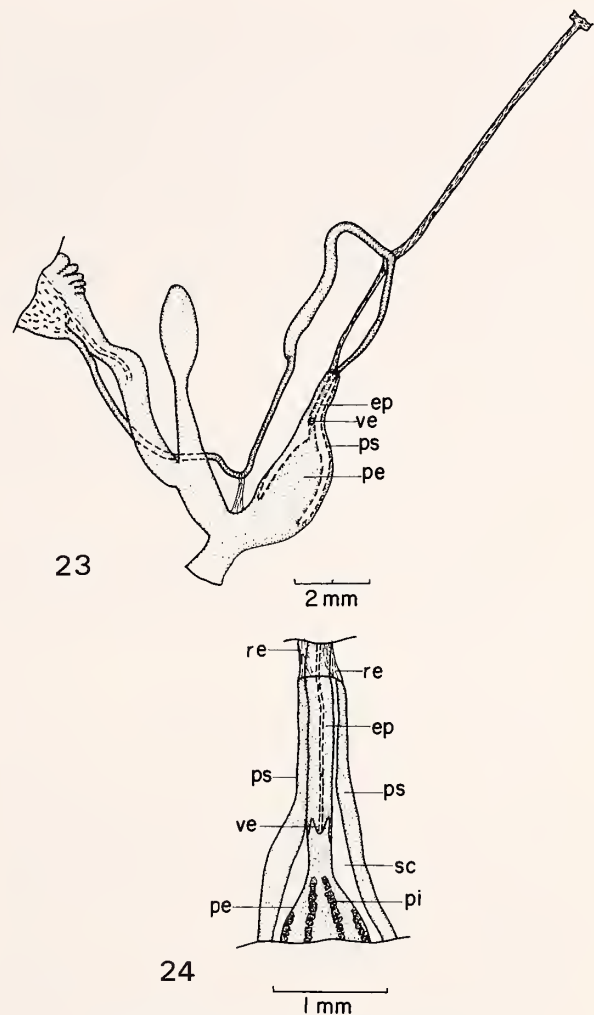
Verge within narrow, tubular, apical portion of the penis, about 0.15 to 0.20 mm long, 0.20 mm wide at base (Figure 24). Seminal duct opening into penis through tip of verge.

Spermathecal duct small and narrow, tightly appressed to free oviduct, which is of equal diameter and branches from it, cylindrical-conic, about 2.0 mm long, about 0.7 mm in diameter at junction with oviduct, tapering gradually to 0.3 mm constriction at base of spermatheca.

Spermatheca oblong-ovate in fully mature specimens, narrowly cylindrical in less mature individuals, about 2.7 mm long, with rounded tip.

Type material: Holotype: SBMNH 34203, CALIFORNIA: El Dorado County: canyon of South Fork of American River near Riverton.

Paratypes: CAS 064120, CAS 066614, SBMNH 34204, from same locality as holotype.



Explanation of Figures 23 and 24

Figures 23, 24. *Vespericola orius* (Berry). Drawings made from projections of stained whole mounts. Figure 23. Anterior portion of reproductive system, SBMNH 36097, CALIFORNIA: El Dorado County: along left bank of North Fork of Cosumnes River at crossing of Cosumnes Mine Road, W. B. Miller coll., 21 January 1991. Figure 24. Enlarged section of epiphallus and apical portion of penis to show location of verge, SBMNH 36098, collection data same as above.

Distribution: CALIFORNIA: El Dorado County: Placerville (CAS); near Camp Creek, 4.8 km E of Pleasant Valley (CAS); along left bank of North Fork of Cosumnes River at crossing of Cosumnes Mine Road, W. B. Miller coll., 21 January 1991 (SBMNH); Eagle King Mine, near Grizzly Flat (CAS, BR); South Fork of American River near Riverton (CAS).

Remarks: The epiphallus and the apical part of the penis form a continuous tube of constant diameter, with no external differentiation. There is no bulge or swelling at the level of the verge. Only at about 0.5 mm below the verge does the penis enlarge abruptly into a capacious cavity.

This gives the appearance that the verge is located well up in the epiphallus; but, by convention, the portion of the male sperm-delivering duct below the base of the verge and above the atrium, everted in copulation, is defined as the penis. It seems probable to us that the slender part of the duct below the base of the verge is homologous with the summit of the penial sac in other species of *Vespericola*.

Vespericola orius is distinguished anatomically from other species by its minuscule verge located in a narrow, tubular, prolongation of the apex of the penial chamber; by its short, stout penis in a penial sheath overlapping a sizeable part of the epiphallus; and by its small, narrow spermathecal duct.

The inner end of the basal lip of the aperture is more distinctly angled forward than in *Vespericola pilosus* and covers, on the average, less of the umbilicus. The surface between the periostracal setae is less granulose than in *V. pilosus*, especially on the spire.

For purposes of the American Fisheries Society list of the common names of mollusks (TURGEON *et al.*, 1988) and other administrative uses, we propose the name "El Dorado hesperian."

OTHER RECORDS OF *Vespericola columbianus* IN CALIFORNIA

In museum collections, shells in which the inner lip is not markedly dilated over the umbilicus are often identified as *Vespericola columbianus*. On the basis of our previous findings, we believe such identifications require confirmation by dissection.

PILSBRY (1940) reported *Vespericola columbianus pilosus* from Crescent City, Del Norte County, and San Pablo, Contra Costa County, California. Our collecting along the coast of Del Norte County has not turned up any *V. columbianus*, but rather *Vespericola megasoma*, *Vespericola euthales* (Berry, 1939), and two new species, outwardly similar to *V. megasoma*, that will be described and discussed in a future paper.

Museum collections contain samples resembling *Vespericola pilosus* from several localities in Contra Costa and Alameda counties. The shells are, in general, more depressed and more widely umbilicate than those of *V. pilosus* from the San Francisco Peninsula, with the inner part of the basal lip angled rather sharply forward. A parietal lamella is absent. We are in the process of trying to locate living populations for anatomical data.

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